

THE SHRUBBY GENTIAN GENUS *MACROCARPAEA* IN PANAMA

KENNETH J. SYTSMA¹

ABSTRACT

A single species of the lisianthoid genus *Macrocarpaea* had been known from Panama. Recent explorations of previously inaccessible cloud forest peaks in western, central, and eastern Panama have turned up additional species previously known only from Costa Rica and Colombia. Three species are now recorded from Panama: *M. browallioides*, *M. macrophylla*, and *M. subcaudata*. Evidence is provided to merge the Costa Rican *M. valerii* into *M. macrophylla*.

The shrubby gentians of the Neotropics are some of the most conspicuous elements of higher elevation tropical forests. This complex of about 16 genera comprised Grisebach's (1838) tribe Lisyantheae. These lisianthoid genera are notoriously difficult to separate taxonomically with the consequence that they have often been treated as synonyms of *Lisianthus* (or its orthographic variant "*Lisianthus*"). The taxonomic difficulties are compounded by their remote montane habitat which makes them poorly collected. Only *Lisianthus* sensu stricto (Weaver, 1972a) and *Macrocarpaea* (Ewan, 1948) have been adequately monographed. Other genera of the tribe Lisyantheae are now being taxonomically revised in a multidisciplinary study (Maas et al., 1984; Maas, 1985).

Macrocarpaea (Griseb.) Gilg is one of four lisianthoid genera in Panama (Elias & Robyns, 1975). *Symbolanthus pulcherrimus*, *Irlbachia alata* subsp. *alata* (formerly *Chelonanthus alatus*), and seven species of *Lisianthus* (Sytsma, 1987) also occur in Panama. These four genera can be separated in Panama by the following characteristics:

- 1a. Main stem terete; stigma capitate; old placentae visible as whitish bands along margins of mature capsules; pollen grains as monads *Lisianthus*
- 1b. Main stem usually quadrangular; stigma bifurcate; old placentae not visible on mature capsules; pollen grains as monads or tetrads.
 - 2a. Flowers 6–10 cm long; corolla funnel-form; more or less distinct, membranaceous; corona scalelike; pollen grains as tetrads *Symbolanthus*
 - 2b. Flowers to 5 cm long; corolla usually campanulate; corona absent; pollen grains as monads or tetrads.
 - 3a. Leaves sessile; bracteoles never

- leafy; calyx 4–6 mm long; pollen grains as tetrads *Irlbachia*
- 3b. Leaves petiolate; bracteoles leafy; calyx 6–20 mm long; pollen grains as monads *Macrocarpaea*

The genus *Macrocarpaea* is centered in the Andes of northern South America but extends into the Amazon Basin and the Guayana Highland. Of the approximately 30–50 species in the genus, only eight are known from Central America and adjacent West Indies. *Macrocarpaea domingensis* Urban & E. Ekman and *M. thamnoides* (Griseb.) Gilg are restricted to the Dominican Republic and Jamaica, respectively. Cuba has two endemic species, *M. pinetorum* Alain and *M. pauciflora* Alain. Three species have been described from Costa Rica (Weaver, 1972b): *M. subcaudata* Ewan, *M. valerii* Standley, and *M. acuminata* Weaver. A single species, the endemic *M. browallioides* (Ewan) Robyns & S. Nilsson, has been known from Panama near the border of Costa Rica (Elias & Robyns, 1975). The type specimen had represented the only collection for this apparently epiphytic shrub prior to 1975.

Recent explorations of cloud forest habitats in central regions of the Cordillera Talamanca, a ridge extending from the border of Costa Rica to near Panama City, and in the Cordilleras of the Darién near Colombia have provided additional sites for the previously known *Macrocarpaea* and new *Macrocarpaea* species for Panama. These explorations were conducted under the auspices of the Missouri Botanical Garden through the Flora of Panama Project (funded by NSF grant BSR-8305425). *Macrocarpaea subcaudata*, an epiphytic shrub known previously from only two collections in one region of Costa

¹ Botany Department, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

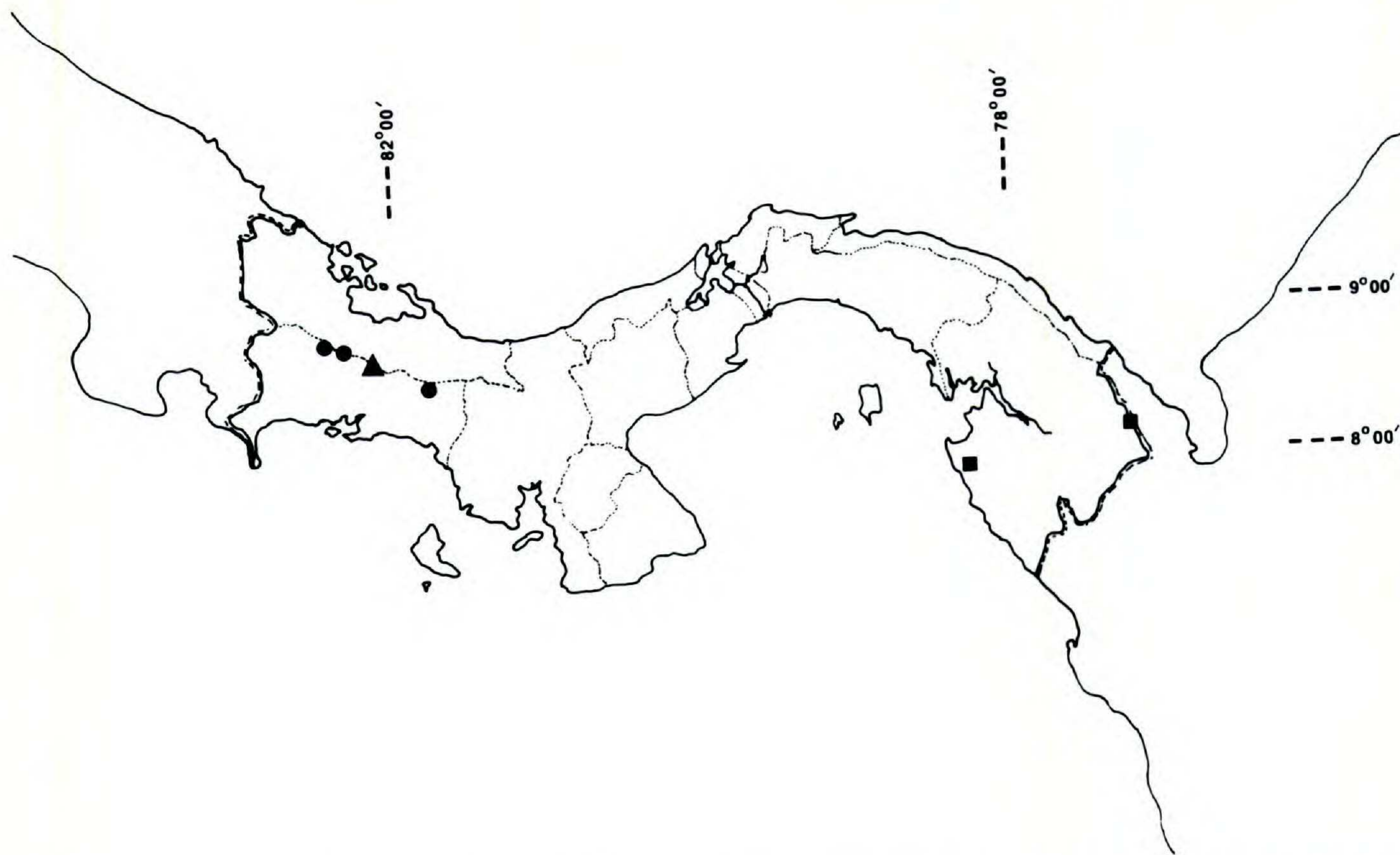


FIGURE 1. Geographical distribution of the genus *Macrocarpaea* in Panama. Circle = *M. browallioides*; square = *M. macrophylla*; triangle = *M. subcaudata*.

Rica, occurs in one cloud forest region in the mountains of central Panama. Recent additional collections of *M. browallioides* now extend the range of this distinctive epiphytic shrub. Several populations similar to both the Costa Rican *M. valerii* and the Colombian *M. macrophylla* (Kunth) Gilg are now known from the Darién. Analysis of morphological variation among the Costa Rican, Panamanian, and Colombian populations provides a basis for merging *M. valerii* with the now more widespread *M. macrophylla*.

KEY TO *MACROCARPAEA* IN PANAMA

- 1a. Calyx 6–14 mm long, lobes ovate-oblong, rounded at apex.
 2a. Epiphytic viny subshrub, leaves narrowly lanceolate, to 18 cm long and 5 cm wide 1. *M. subcaudata*
 2b. Terrestrial shrub to 4 m, leaves broadly elliptic, to 45 cm long and 26 cm wide 2. *M. macrophylla*
 1b. Calyx 15–18 mm long, lobes triangular, acute to cuspidate at apex 3. *M. browallioides*

1. *Macrocarpaea subcaudata* Ewan, Contr. U.S. Natl. Herb. 29: 224. 1948. TYPE: Costa Rica: [San José] La Palma, Wercklé 16492 (holotype, US; isotype, NY).

Epiphytic, viny subshrub. Leaves essentially glabrous except for small scattered hairs, somewhat thickened, narrow-lanceolate, to 18 cm long and 5 cm wide; petioles to 23 mm long. Inflorescence terminal or axillary from upper nodes, dichasium bi- or tri-ternately compound, often long-stalked. Calyx campanulate, greenish, glabrescent, 6–9 mm long; lobes slightly unequal, ovate-oblong, rounded or ciliolate at tips, 5–7 mm long, 3–4 mm wide. Corolla greenish yellow, to 3 cm long; tube to 2.3 cm long; lobes slightly recurved (incurved when dried), narrowly triangular, to 9 mm long, to 6 mm wide. Stamens inserted near middle of corolla tube; filaments to 17 mm long, just surpassing corolla lobes; anthers yellow, 4–5 mm long. Style just surpassing anthers. Capsules woody, 10–12 mm long ex. persistent beak of 3 mm. Flowering period at least mid-April through May.

Distribution. 1,500 m in mountains east of San José, Costa Rica and between 1,150–1,260 m near continental divide between Chiriquí and Bocas del Toro provinces in central Panama (Fig. 1).

Additional specimens examined. PANAMA. BOCAS DEL TORO: Continental divide on carretera del oleoducto ca. 1 km N of Quebrada Arena, IRHE Hydro-

electric Project, *Knapp 5089* (MO), *McPherson 8613* (MO). CHIRIQUÍ: Along road between Gualaca and IRHE Hydroelectric Project, 10.1 mi. NW of Los Planes de Hornito, *Antonio 4190* (MO).

Macrocarpaea subcaudata occurs only in central Costa Rica and northcentral Panama. Determining whether this disjunction is real or not must await further collecting in as yet inaccessible cloud forest regions of both countries. Relationships of *M. subcaudata* to other species of *Macrocarpaea* are unclear. *Macrocarpaea browallioides* of Panama shares the epiphytic habit with *M. subcaudata*, but the two are clearly unrelated. Ewan (1948) considered *M. cerronis* Ewan and *M. salicifolia* Ewan from the tepuis of the Guayana Highland to be the closest relatives of *M. subcaudata*. The former two species (with related *M. arborea* (Britton) Ewan, *M. quelchii* (N.E. Br.) Ewan, and *M. tepuiensis* (Gleason) Steyerf.), however, differ from all other species of *Macrocarpaea* in having pollen in tetrads (Nilsson, 1968, 1970). Maas (1985) combined these six *Macrocarpaea* species with pollen in tetrads into *Irlbachia quelchii* (N.E. Br.) Maas. Weaver (1972b) cited *M. acuminata* Weaver and two West Indian species as the closest relatives of *M. subcaudata*. The Costa Rican *M. acuminata* is almost certainly related to, if not conspecific with, *M. macrophylla* (including *M. valerii*). *Macrocarpaea acuminata* and *M. macrophylla* share with *M. subcaudata* similar calyx features and might be close relatives of *M. subcaudata*.

2. *Macrocarpaea macrophylla* (Kunth) Gilg, Nat. Pflanzenfam. 4(2): 94. 1895. *Lisianth(i)us macrophyllus* Kunth, Nov. Gen. & Sp. 3: 183. 1819. TYPE: Colombia: trail over paramillo to Almaguer between Pansitara and Río Ruiz, 8,400 ft., *Humboldt & Bonpland* (Willd. Herb. 3561 fide Grisebach; MO photo 37455, of collection in Humboldt Herbarium at Paris).

Macrocarpaea valerii Standley, Publ. Field Mus. Bot. 18: 928. 1938. TYPE: Costa Rica: La Hondura de San José, *Valerio 692* (F).

Erect shrub or subshrub to 4 m tall. Leaves essentially glabrous, except for scattered small hairs, venation strongly prominent, broad-elliptic, to 45 cm long and to 26 cm wide, blade acute or abruptly acuminate; petioles to 3 cm long. Inflorescence terminal or axillary from upper nodes, dichasium simple or bi- or tri-ternately

compound, long-stalked. Calyx campanulate, fleshy, 8–14 mm long; lobes strongly unequal, ovate-oblong, hyaline-margined, 3–6 mm long and wide. Corolla greenish-white or cream, narrowly to openly campanulate, to 3.5 cm long; tube 2.5–3.0 cm long; lobes recurved, broadly triangular, 6–8 mm long and wide. Filaments to 18 mm long, included in or surpassing corolla tube; anthers yellow, 3–5 mm long. Style to 15 mm long; stigma bilobed, the lobes 2 mm long. Capsules woody, to 20 mm long, persistent-beaked. Flowering period at least May through July.

Distribution. 1,000–1,800 m in mountains of Central Costa Rica; 1,000–1,400 m in Serranía del Sapo and Serranía del Darién of Darién Province, Panama (Fig. 1); and common at 1,500–2,500 m in the western and central Cordilleras of Colombia.

Additional specimens examined. PANAMA. DARIÉN: NE slope of Summit, Cerro Sapo, approach from Garachiné, *Hammel 7263* (MO); top of Cerro Mali, 10-year-old second growth on site of old helipad, Serranía del Darién, Panama/Colombia frontier, Cerro Tacarcuna expedition, *Gentry & Mori 13655* (MO), *Gentry et al. 16975* (MO).

Macrocarpaea macrophylla is distinctive as a tall erect shrub with large round leaves and prominent venation. As here defined, *M. macrophylla* ranges from Colombia to Costa Rica. Standley originally described the Costa Rican *M. valerii* based only on the type specimen. Ewan (1948) reiterated the differences between the two species based on only two Costa Rican collections. These differences were confined to size and shape of leaves and to corolla shape. Both sets of characters are subject to sampling error depending on how the plants were collected and pressed. Subsequently, additional collections of “*M. valerii*” in Costa Rica indicated that these features were not consistent, causing Weaver (1972b) to state that “the two are virtually identical, except the calyx of *M. valerii* is glabrous, while that of *M. macrophylla* is spiculate.” Colombian, Panamanian, and Costa Rican specimens of these two taxa at MO and WIS showed considerable variation in the degree of surface ornamentation on the calyx. No consistent calyx differences or other foliar and floral differences were seen among specimens described as *M. macrophylla* and *M. valerii*. This necessitates the inclusion of these Colombian, Panamanian, and Costa Rican specimens into *M. macrophylla* (Kunth) Gilg, the name with priority.

3. *Macrocarpaea browallioides* (Ewan) Robyns & S. Nilsson, Bull. Jard. Bot. Natl. Belgique 40: 13. 1970. *Lisianth(i)us browallioides* Ewan, Proc. Biol. Soc. Washington 64: 132. 1951. TYPE: Panama. Bocas del Toro: northern slopes of Cerro Horqueta, Robalo Trail, Allen 4932 (MO).

Epiphytic shrub to 1.5 m tall. Leaves glabrous, ± coriaceous, dark green and black-punctate above, gray-green below, elliptic to ovate-elliptic, to 11 cm long and to 5 cm wide; petioles to 25 mm long. Inflorescence a compound dichasium, ± long-stalked. Calyx campanulate, light green, 15–20 mm long; tube short; lobes ovate-triangular, strongly overlapping, 12–16 mm long, acute to long-acuminate at apex. Corolla fleshy, yellow-green to cream yellow, infundibuliform, 3.0–4.0 cm long; lobes subequal, ovate-triangular, acute at apex, to 1.2 cm long. Stamens inserted ca. 6 mm above base of corolla tube, ± exserted; anthers yellow, 5–6 mm long. Style just surpassing anthers. Capsule woody, to 14 mm long, excluding persistent beak of 6–8 mm. Flowering in February, May, August, and late November.

Distribution. 1,690–2,200 m, cloud forests of cerros Horqueta, Pate Macho, and Colorado, provinces of Chiriquí and Bocas del Toro.

Additional specimens examined. PANAMA. BOCAS DEL TORO: forest along trail from end of Río Palo Alto road to Chiriquí/Bocas del Toro border near peak of Cerro Pate Macho, Hammel 5781 (MO). CHIRIQUÍ: Cerro Pate Macho, ca. 5 mi. NE of Boquete, trail to continental divide leading to Finca Serrano, Antonio 2654 (MO); Cerro Colorado, along mining road 31.6 km beyond bridge over Río San Felix, 10.6 km beyond turnoff to Escopeta, Croat 37155 (MO); Cerro Pate Macho, along the continental divide, on trail which leads to Finca Serrano, NE of Boquete, Croat 48537 (MO); NW of Pate Macho, Hammel 6112 (MO); NW ridge of Cerro Pate Macho from summit to Finca Serrano, Sytsma et al. 4900 (MO).

Macrocarpaea browallioides is easily distinguished from the other Central American species of *Macrocarpaea* by its large calyx and long-acuminate calyx lobes. Like *M. subcaudata* it is epiphytic, but unlike *M. subcaudata* it is erect rather

than viny. Several of the collectors do not mention an epiphytic habit. However, the distinction between an epiphytic and terrestrial habit is tenuous on an extremely wet, peatlike soil as is encountered on Cerro Pate Macho. True epiphytic as well as free-standing (although on mats of living roots or trunks) individuals of *M. browallioides* were seen on this cloud forest peak. The relationship of this species to other members of *Macrocarpaea* is unclear. Neither Ewan, who first described the species as a *Lisianthus*, nor Robyns and Elias, who transferred it to *Macrocarpaea*, gave any indication as to its likely relatives. Only three known species approach *M. browallioides* with its distinctive short calyx tube and long, overlapping, and acuminate-tipped lobes: *M. cochabambensis* Gilg of Bolivia; *M. glabra* (L.f.) Gilg endemic to paramo vegetation above Bogotá, Colombia; and *M. guttifera* Ewan of Amazonia, Brazil.

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